Funded by
the European Union

Australia’s National
Science Agency

Evaluation of potential close-kin mark recapture sampling designs for Indian Ocean shortfin mako shark

IOTC Working Party on Ecosystems and Bycatch

September 2025

Toby A Patterson, Pia Bessell-Browne

IOTC-2025-WPEB21(AS)-42

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Summary

This paper presents the results of a statistical design exercise investigating the potential for Close-kin Mark-recapture (CKMR) to provide accurate assessment of population size for Indian Ocean shortfin mako sharks (*Isurus oxyrinchus*). CKMR uses the prevalence of closely related animals (in this study, those which share a parent) in a collection of genetic samples to estimate adult population size. The method can be combined with more typical fisheries data in order to conduct integrated stock assessments. Prior to committing to a large scale CKMR study, it is prudent to conduct a numerical design exercise to investigate how many sample sizes are likely to be required, assuming current knowledge of a population is informative enough to at least guide planning of real sampling. In this working paper, we provide some introductory desciption of how CKMR operates and then detail a design approach to investigate sampling strategies for SMA. For this, a sex and age-based operating model was constructed that simulated CKMR kinship data and catch-at-age data. These data were fed into a similarly structured statistical estimation model which estimated population parameters and predictions of spawning output (akin to spawning stock biomass) and other quantities. The operating model was tuned to approximate outputs from the 2024 stock assessment. We considered a range of sample sizes, which recent IOTC data would suggest are logistically feasible to obtain - even if there are now complications in retaining samples from current management measures. The design modelling estimated that informative population estimates (i.e. with sufficiently low uncertainty to be useful in management decisions) would be expected from 2000 annual samples over 5 years. Testing of this approach with 1000 tissue samples were predicted to be of a reduced quality, and we advise any future sampling program to aim for at least 2000 samples per year. We outline the results and discuss challenges and opportunities for initiating CKMR at scale to obtain estimates of population size for SMA and other pelagic sharks captured by Indian Ocean fishing operations.

1 Introduction

The shortfin mako shark (*Isurus oxyrinchus*, SMA) is a large pelagic shark with a circum global distribution over a latitudinal range of approximately 50°N to 50°S. It has a low biological productivity owing to a slow reproductive cycle and late age at maturity (Bowlby et al. 2022).

Various analyses have concluded that SMA is highly susceptible to longline fisheries (Murua et al. 2018). The catch data used in Coelho et al (2024) (combined records of SMA, Mackerel sharks and Porbeagle) from the IOTC indicate catches in recent years to be in excess of 2000 tonnes, down from a peak of approximately 5400 tonnes in 2014. Globally, most catches are focused on juveniles and large adults are rarely captured. However, concerns about ongoing declines center around the possibility that largely juvenile catches are not allowing for replenishment of adults (Kai 2021; Bravington 2019).

Globally, there is poor knowledge of the species status, but is generally thought to be declining (Sims, Mucientes, and Queiroz 2021). As such, the species is listed as Endangered under IUCN rankings and is listed under CITES Appendix II, although there has been debate regarding the efficacy of this as a management response (Kai 2021; Sellheim 2020).

Globally, stock assessments of SMA have faced data uncertainty and inconsistencies and have mainly applied surplus production model approaches to calculate stock status (Anon 2019; Anon. 2024). In the Indian Ocean, the 2024 assessment of Coelho, Rosa, and Mourato (2024) was conducted using a Bayesian surplus production model (the JABBA methodology Winker et al. (2020)). This is the most recent assessment for the Indian Ocean and the base-case suggested that the stock is currently overfished and subject to overfishing, albeit with large uncertainty. This assessment also recommended that there is a need to reduce catches to a total allowable catch at 40% of current levels to prevent further declines in stock size (Coelho, Rosa, and Mourato 2024).

Given general concern at the potential for current catch levels leading to overfishing of SMA, and that current estimates of stock status are highly uncertain, there is a need to explore new approaches that will allow for a greater degree of certainty about stock size to guide future management decisions.

This paper details a statistical design study examining the feasibility of using close-kin mark recapture (CKMR) to assess shortfin mako in the Indian Ocean (Bravington, Skaug, and Anderson 2016). We first provide a brief overview and context for CKMR and then consider a very simple examination of potential sample sizes before presenting the details of a more complex approach based on using CKMR data along with catch-at-age data in an age-structured assessment model. Further details on the practical requirements of sample collection, sequencing methods and potential sample sources are given in Patterson et al, IOTC-2025-WPEB21(AS)-41.

1.1 CKMR background

CKMR is a relatively new stock assessment method that has been demonstrated to be a powerful technique for estimating animal abundance (Bravington, Skaug, and Anderson 2016; Bravington, Grewe, and Davies 2016; R. M. Hillary et al. 2018; Ruzzante et al. 2019). In essence, CKMR is a mark recapture technique based on data from modern genetic sequencing methods. This data allows kinship between pairs of sampled individuals to be used as a mark. The method has now been used on several elasmobranch species (R. M. Hillary et al. 2018; Bruce et al. 2018; Patterson, Hillary, Feutry, et al. 2022; Patterson, Hillary, Kyne, et al. 2022; Bradford et al. 2018; Trenkel et al. 2022; Thomson et al. 2020)

Because CKMR uses the DNA of the animal as a tag, it is less susceptible to fisheries catch reporting biases and under-reporting than traditional methods, and is entirely fisheries independent (Bravington, Skaug, and Anderson 2016). The method produces estimates of sex-specific adult abundance and trend therein, as well as adult mortality rates. While it does not need other data sources, such as catch-at-age/length data, these can be combined with CKMR data in integrated assessments (Thomson et al. 2020; Hillary et al. 2023; Punt et al. 2024) and Management Strategy Evaluation (Hillary, Preece, and Davies 2017).

The premise for CKMR is that number of kin-pairs in a sample of individuals is inversely related to the size of the breeding population. If a study finds a high rate of kin-pairs per sample, this suggests a smaller population than a lower rate of kin-pair detection. This is the central idea of CKMR and in the simplest (and most unrealistic) setting of a closed population with no mortality, recruitment, emmigration or immigration, it is a form of Lincoln Petersen estimate (Bravington, Skaug, and Anderson 2016).

Real world applications of CKMR are generally more complex than this (e.g. Hillary et al. 2023). One of the reasons for this complexity is that the probability of detecting a given number of kin-pairs is related to the expected total reproductive output (TRO) of the adult population. Therefore, in relating kinship data to abundance, the population dynamics model usually has to account for factors such as maturity schedules, reproductive output, selectivity in the sampling, among other factors (Bravington, Skaug, and Anderson 2016). Additionally, the influence of these covariates may need to be sex specific.

These complexities notwithstanding, CKMR is a type of natural tagging experiment which is fisheries independent and, therefore, is not subject to problematic reporting rates, fleet/gear/targeting changes, errors in catch reporting and other potential sources of bias associated with more traditional fisheries and mark recapture data (Polacheck and Davies 2007). The attractiveness of CKMR is that it can provide an estimate of absolute abundance of the breeding population from a relatively short study (possibly over a few years) and, with enough data, can simultaneously provide estimates of adult mortality rates and population trend.

Another key point is that for sizeable pelagic fisheries, CKMR is also cost effective relative to other methods such as large-scale/long-term conventional tagging programs (Kolody and Bravington 2019). Additionally, when CKMR studies are conducted at appropriate scale, it is also one of the fastest methods for obtaining abundance estimates. Estimates of population size and trend can be produced from a research program of several years. This feature of CKMR derives from the fact that the population has already “tagged itself” through its DNA. A conventional tagging program, even putting aside the aspects of logistics, expense, tag reporting/loss etc., produces data in “real time”. For long lived species such as sharks, this can mean that informative data for traditional abundance estimation are slow to accumulate.

CKMR typically consider two instances of kinship; Parent-offspring-pairs (POPs) and sibling pairs, where two individuals share at least one parent. If one parent is shared this is termed a half-sibling pair (HSP), and if both parents are shared then this is termed a full-sibling pair (FSP). As we will expand on below, a key quantity is the probability of finding a kin pair given both the underlying stock abundance and dynamics, and the amount of sampling effort.

FSPs are typically not used in CKMR, while POPs and HSPs provide slightly different information in CKMR population models. POPs primarily inform estimates of relative reproductive output which can be linked to abundance, while HSPs also carry a signal of total mortality.

The modelling here considers HSPs as the sole type of kin data. This is because juveniles are the overwhelming proportion of the catch (see Patterson et al., IOTC-2025-WPEB21(AS)-41). As described in Bravington (2019), by comparing over a time series of cohorts, HSPs can be used to find abundance. This is because the average rate of finding HSPs is inversely proportional to the average adult abundance. The rate here is the proportion of the pairwise comparisons between all samples that are HSPs. Changes in the HSP detection rate for new cohorts signals how fast the adult population is changing. Additionally, the rate of change in HSP detection rates over a given cohort gap is an information source on total adult mortality (Z).

Among other concerns, is the accuracy of SMA catch data in the Indian Ocean (IO), because very few adults are captured it is difficult to monitor status and trends in the spawning stock. This is one of the major motivations for considering CKMR - as a key advantage of the method is its ability to estimate adult numbers and mortality rates from sampling of juveniles.

As we demonstrate in the model used here, while CKMR alone estimates total mortality (Z), this can be split into natural mortality (M) and fishing mortality (F or alternatively a harvest rate h, as used here), if data on catches and catch-at-age/size are available. Further complications can be considered such as spatial structure as HSP detection rates between areas inform on spatial connectivity (Hillary et al. 2022).

1.2 Preliminary calculations: Could CKMR work?

Before embarking on a detailed design exercise, it can be instructive to examine whether there is any appreciable chance of obtaining a useable number of HSPs from a population resembling what we guess SMA might look like in terms of number of mature individuals. To complete this calculation, an estimate of total reproductive size is required. As there is no basis for an estimate in the following, we simply examine a range of populations sizes from 10-800K adults. To do this we assume each adult has the same expected reproductive output, a 50:50 sex ratio and the following:

- An average time of δ_t between HSP birth years
- A constant total mortality rate of Z
- A constant N_A number of adults with equal reproductive output

- Sample size of N_S
- There are no births, deaths or immigration/emmigration over the sampling period.

Given these highly unrealistic assumptions, the HSP probability given a 50:50 sex ratio for either sex $p_{hsp} = 2/N$ (as every juvenile has 2 parents) and so for HSP in general $p_{hsp} = 2/N_A + 2/N_A = 4/N_A$. This factor has to be adjusted for mortality effects on the adults over δ_t which is used in the formula below. From this we can calculate the expected number of HSPs as $N_{HSP} =$ HSP probability $\times$ N(pairwise comparisons) which is given by:

$$N_{HSP} = \left(4e^{-Z\delta_t}/N_A\right)\left[\frac{N_S(N_S-1)}{2}\right]$$

If we set the desired number of HSPs (see below) we can therefore solve for the number of samples S as

$$N_S = \frac{1+\sqrt{1+2\ N_A\ N_{HSP}\ e^{-Z}}}{2}$$

We can set the required numbers of half-sibling pairs, N_{HSP} (e.g. 50, 100) by noting that the coefficient of variation on an estimate scales roughly as $CV(N) = 1/\sqrt{N_{HSP}}$. Therefore, we would need at least 25 (CV of 20%) for a poor estimate. Using this argument with some plausible guesses for Z and δ_t and running over a range of adult population sizes and numbers of HSPs, we get the results in Table 1.1. This shows that if the population is small, and an imprecise estimate is sufficient, then few samples are required (Table 1.1).

These results also highlight an important aspect of CKMR in that a larger population requires a higher number of samples to get an equally precise result. Therefore, in the context of a species where there is a concern of over depletion, for a given number of samples, there will be more precise indications of “bad news” and conversely, imprecise evidence of “good news”.

Table 1.1: Simple calculations of number of samples, N_S (cell values) that would be required to estimate number of adults (rows). Here Z = 0.26 (which is an annual survival rate of adults of S= 0.77 y^{-1}) and δ_t= 4 years.

N(adults)	**N[HSP]= 25 (CV= 0.2)**	**N[HSP]= 50 (CV= 0.14)**	**N[HSP]= 100 (CV= 0.1)**
50,000	471	665	941
100,000	665	941	1330
200,000	941	1330	1881
300,000	1152	1629	2303
500,000	1487	2102	2973
800,000	1881	2659	3761
900,000	1995	2821	3989

2 Population / Operating model

We implemented an age- and sex-structured population dynamics model (the Operating Model, OM) based on SMA biology and demographics. The OM was tuned to replicate key aspects of the 2024 IOTC stock assessment given the time series of catches (also used in the assessment, Coelho, Rosa, and Mourato (2024)).

The model used in this study generates two potential sources of information; (1) the kinship data that would be derived from sequencing of tissue samples and detecting HSPs and (2) information on the distribution of catch-at-age. This can come from the same sampling program - i.e. we assume measuring ages (or converting measured lengths to age) occurs at the same time as samplers take a tissue sample.

Conditional on the underlying population abundance and age distribution, we simulated the number of half-sibling pairs (HSP, CKMR data) and catch-at-age (CAA data) samples that would be expected given the underlying population dynamics and a candidate sampling design.

2.1 Caveats on the design approach

Design studies for CKMR can consider potential uncertainties in fundamental data such as the effect of ageing error (RM Hillary et al. 2022). In these examples, there is often a comprehensive set of stock assessment outputs and, therefore, a better understanding of the population status. For SMA in the IOTC region, estimates of numbers at age are not available. Additionally, in a similar design study for SMA in the Atlantic, Bravington (2019) found that ageing error had surprisingly little effect on the uncertainty of management metrics. For these reasons and to maintain simplicity we have not considered the effect of ageing error in this study.

Additionally, following Hillary et al. (2022) we do not consider geno-typing related errors or false negative/positive rates in kin-pair detection and, therefore, assume that any kin in a sample will be detected without error. In reality, these assumptions are unlikely to hold completely. However, CSIRO experience with sharks on recent studies has found that improvements in sequencing are reducing the influence of these factors. Furthermore, if an actual CKMR study were to be commenced on SMA, detailed examination of these factors would be part of the quality control checks used by CSIRO in reducing the potential for biases due to mistakenly including false positive kin pairs.

2.2 Simulation and estimation approach

The design methodology in this study differed from the previous CKMR design study presented to IOTC Hillary et al. (2022) in that instead of applying analytical statistical information-based approaches to estimate likely uncertainty, we employed a simulation and back-estimation method. Synthetic data sets were generated from an operating model, the OM which were used as input into an estimation model, the EM. While they are simpler, the underlying population dynamics were similar and the CKMR statistics follow the approach of Hillary et al. (2022). The simulation/back-estimation approach has the advantages of being able to examine potential biases due to sampling and also consider fitting other model variants to simulated CKMR data.

So in our study, simulated data generated from the OM was then passed to an EM, which estimated parameters through standard numerical minimization of the joint negative log-likelihood of population parameters and thereby predicted key estimates of such as an estimated adult abundance series (number of mature animals).

These predicted outputs from the EM (parameters and predicted abundances) were then compared to the true simulated versions of these from the OM to compute statistics summarizing the likely uncertainty, potential biases etc.

Given the lack of data on SMA and, therefore, the lack of a full age structured assessment, the OM used here is relatively simple. It is a two-sex, non-spatial model, with a simple density independent stock-recruitment relationship based on litter size and pupping frequency. Where possible model parameters were selected to be consistent with the IOTC surplus production assessment of Coelho, Rosa, and Mourato (2024). For other components, model parameters were drawn from the literature.

The OM was informally "tuned" to approximate the predictions of exploitable biomass from Coelho, Rosa, and Mourato (2024), with sensitivity to this value tested by including scenarios of exploitable biomass at the upper and lower credible intervals of the base case assessment. The same catch series was used as an input.

Details of the model structure are given below.

2.3 Biology

Standard functional forms were used to model growth, maturity and weight-given-age. The proportion of mature animals as a function of age was given by a logistic function:

$$\Pr(mature|a) = m_{s,a} = \frac{1}{1 + 19^{(a_{50}^{s} - a)/(a_{95}^{s} - a_{50}^{s})}}$$

where a_{50}^{s} and a_{95}^{s} are the ages of 50% and 95% maturity, respectively for sex $s = \{female, male\}$.

The expected weight given age was given by:

$$W_{s,a} = a_s L_a^{b_s}$$

where L_a is the expected length given age which was specified by a Von Bertallanffy growth function:

$$L_t = L_\infty \left(1 - \exp\left(-\kappa(a - t_0)\right)\right)$$

Parameters of the weight length relationship were from Romanov and Romanova (2009) and the VBGF parameters were from Liu et al. (2018) (see Table 2.1). Where possible, the the parameter values that were used in the analyses matched those used in the base case of the most recent stock assessment Coelho, Rosa, and Mourato (2024). Parameter values used in the simulation are detailed in Table 2.1 and Figure 2.1.

Table 2.1: Life history parameters used in the simulations.

Life History	Parameter	Sex	Value	Reference
Growth	Linf		323.8	Liu et al. (2018)
	k		0.075	
	t0		-4.36	
Lifespan	max age		32	Coelho et al (2024)
Mortality	M		0.17	Assumed / tuning
Weight-Age	a		0.0000349	Romanov & Romanova 2009
	b		2.76544	
Maturity	a50	F	15.0	Cliff et al. (1990), Francis and Duffy (2005), Bishop et al. (2006), Natanson et al. (2006)
	a95	F	19.	
	a50	M	5.0	
	a95	M	6.0	
Reproduction	N pups		12	Groeneveld et al (2014) (mean value, rounded)
	Pupping frequency		2 years	Mollet et al (2000)
	sex ratio		0.5	Coelho et al (2024)
	recruitment variability		0.1	Assumed

There seems to be various views in the literature on whether the number of pups produced in a SMA litter varies with female size. For this study we assumed a constant litter size (Table 2.1) using estimates from Groeneveld et al. (2014). Pupping frequency of 2 years follows Mollet et al. (2000) a 50:50 sex ratio at bith. As the model is sex-specific maturity, seperate male and female maturity schedules were applied (Table 2.1) based on examination of various literature sources (Cliff, Dudley, and Davis 1990; Francis and Duffy 2005; Bishop et al. 2006; Natanson et al. 2006)

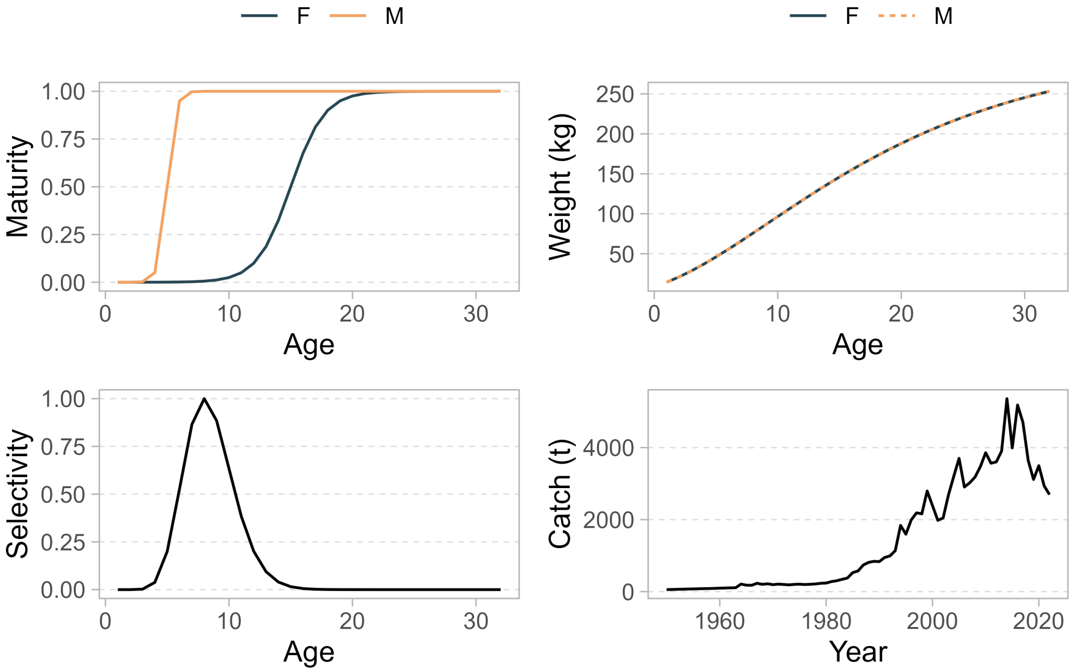

Figure 2.1: Marurity at age, weight at age, selectivity and catch values used in the design study.

2.4 Population model

The population dynamics were structured by sex s, age a and year y and specified by:

$$N_{s,a,y} = \begin{cases} R_y e^{-r_y} & \text{if } a = 1 \\ N_{s,a-1,y-1} e^{-M}\left(1 - h_{s,a-1,y-1}\right) & \text{if } a > 1 \end{cases}$$

where recruitment R_y is given by:

$$R_y = \eta \sum_a N_{f,a,y}\, m_a \gamma / t_{pup}$$

Here η is the sex ratio at birth, γ = expected number of pups per litter and t_{pup} is the spawning interval between litters for females (Table 2.1). Recruitment deviations were modeled as log-normal random variables $r_y \sim \mathcal{N}(0, -(\sigma_R/2)^2)$.

The model is initialised by supplying a starting number of females N_0^f and an initial catch value C_0. In the initial conditions, these two numbers are used to numerically estimate an initial value of harvest rate h_{init} that sets the population at a stable age structure in the first year. In subsequent model years, the total harvest rate in year y is $h_y = C_y/X_y$ where the selected biomass, X_y is:

$$X_y = \sum_s \sum_a N_{s,a,y}\, e^{-M} s_a W_{s,a}$$

where Selectivity s_a is selectivity at age (see below) and $W_{s,a}$ is the expected weight-at-age calculated by combining the VBGF and length-weight relationships. The sex/age specific harvest rate is then:

$$h_{s,a,y} = h_y s_{a,y}$$

Selectivity s_a was modeled as a dome-shaped function (Hulson and Hanselman 2014) of two parameters; a_{max} which is the age of maximum selectivity and a shape parameter b. The selectivity as a function of age is then given by:

$$s_a = \left(\frac{a}{a_{max}}^{(a_{max}/p)}\right) e^{(a_{max}-a)/p}$$

where

$$p = \left(2\sqrt{a_{max}^2 + 4b^2} - a_{max}\right)^{-1}$$

Tuning the OM to approximate the results of the most recent stock assessment was done in terms of the estimated exploitable biomass (Coelho, Rosa, and Mourato 2024) for years after 2020. The parameters that were allowed to vary to meet the conditioning constraints were the overall number of females in the population and the initial harvest rate. Due to differences in the structure of the biomass dynamics model implemented by Coelho, Rosa, and Mourato (2024) and the age-structured population dynamics developed here, it was not possible to directly match the results of the stock assessment. We have, however, matched the absolute value as closely as possible, while trends through time differ slightly.

Due to the large credible intervals on exploitable biomass $B_{exp,y}$ from the 2024 JABBA assessment, we have tested three scenarios of population size, one around the median estimate from the base case 2024 IOTC stock assessment, one approximately at the upper 95% credible interval and one approximately at the lower 95% credible interval.

2.5 Estimation model (EM)

The EM had the same population dynamics as the OM but requires characterization of various quantities related to kinship likelihood based on various calculations related to age-specific reproductive output. Accordingly, the following section details how, given the population dynamics outlined above, we both simulate Half-Sibling Pairs (HSPs) from a population, and also use the same quantities in calculating the likelihood of an observed number of HSPs so that we can estimate population quantities from HSPs.

2.5.1 Half-sibliing probabilities given population dynamics

For CKMR the model must track the expected relative-reproductive output given relevant covariates such as age, size, sex. The following quantities are required for calculating the likelihood of kin matches arising from a random sample of the population as would be the case in a study. These same quantities are also required for calculation of the statistical likelihood of a given number of kin-matches.

Given the biology of SMA, a simple model of relative spawning output at age $\phi_{s,a}$ was used where the expected per-capita pupping output at age is scaled relative to the maximum over age. How this relates to concepts of spawning stock biomass in general is discussed in Hillary et al. (2022). In sharks, reproductive output often does not vary with age to the exent seen in teleosts, which led to the simpler model given here as

$$\phi_{s,a} = \frac{m_{s,a}\gamma/t_{pup}}{\max_{a}[m_{s,a}\gamma/t_{pup}]}$$

The reproductive potential (or TRO - which here gives an estimate of spawning stock size - since reproduction at age is considered constant- is given as:

$$S_{s,y} = \sum_{a} N_{s,a,y}\,\phi_{s,a}$$

The adult age-distribution is calculated as

$$g_{s,a,y} = \frac{N_{s,a,y}\phi_{s,a}}{S_{s,y}}$$

2.5.2 Simulation and likelihood calculations

Simulation of data from the data-generating models based on the underlying OM dynamics and back-estimation of model parameters and population state, both require calculation of the same two probabilities. Specifically, these are:

1. p_{HSP}: The probability of an observed number of kin deriving from two comparison candidate years
2. p_{CAA}: The probability of observed catch-at-age data given harvest rates and age-specific selectivity.

2.5.3 CKMR simulation and likelihood calcuations

Following details given in Hillary et al. (2022), to calculate p_{HSP} for a given comparison of individuals born in cohorts c_i and c_j, we need to consider the following quantities:

1. At the time of birth of the older juvenile, what is the sex and age distribution of adults that could have been the parents?
2. Given total mortality (M and F), what is probability that a potential parent survived over $\Delta c_{ij} = c_i - c_j$, the elapsed time between i and j's birth years?
3. At the time of birth of the younger juvenile, what is the probability that a given parent out of all other potential parents, was the actual parent of the younger juvenile?

The individual parents are of course, unobserved. Therefore, calculation of the p_{HSP} integrates over all possible age, and informally, the probability of a half-sibling pair combines the three components listed above as:

$$p_{HSP} = (\text{dist. possible parent age}) \times \Pr(\text{parent survived}) \times \Pr(\text{particular parent})$$

which results in the following equation

$$p_{HSP} = \sum_{s \in m,f} \sum_{a=1}^{a_{max}} \phi_{s,\Delta c} \left(\prod_{a} e^{-M} \left(1 - h_{s,a+\Delta c,y_{min}}\right) \right) \left(\frac{g_{s,a,y_{min}}}{S_{s,y_{max}}} \right)$$

To simulate the number of HSPs we would expect from a given comparison of $\{c_1, c_2\}$ we simulate data with the following

$$N^{K}_{c_1,c_2} \sim \text{rbinom}\left(N^{C}_{c_1,c_2}, p_{HSP}\right)$$

where rbinom denotes a random binomially distributed variable. Here $N^{K}_{c_i,c_j}$ are the expected number of kin pairs from the $N^{S}_{c_i,c_j}$ samples compared in the cohort year pair $\{c_i,\ c_j\}$. The term $N^{C}_{c_i,c_j}$ is the number of pairwise comparisons deriving from the samples from cohort year pair $\{c_j,\ c_j\}$.

The number of comparisons (i.e. comparing all samples in a relevant cohort pair to all others, but not to itself) is given by

$$N^{C}_{c_i,c_j} = \frac{N^{S}_{c_i,c_j}\left(N^{S}_{c_i,c_j} - 1\right)}{2}$$

Having specified the relevant quantities above, the negative log-likelihood of data

$$\mathcal{L}_{HSP}\left(\theta \middle| \hat{Y}_{HSP}\right) = -\sum_{i} \sum_{j} N^{C}_{c_i,c_j} \ln(p_{HSP}) + \left(N^{K}_{c_i,c_j} - N^{C}_{c_i,c_j}\right) \ln(1 - p_{HSP})$$

2.5.4 Catch at age simulation and likelihood

The model also used catch-at-age data generated from the OM.

$$\hat{p}_{s,a,y} = \frac{N_{s,a,y}\ s_a}{\sum_a N_{s,a,y}\ \ s_a}$$

To generate CAA data from the OM, multinomial draws of N^{CAA} annual samples were taken in the designated sample years.

$$Y^{CAA}_{s,a,y} \sim \text{rmultinom}\left(N^{CAA}, \hat{p}_{s,a,y}\right)$$

Accordingly, the negative-log-likelihood component for use in the EM is given by

$$\mathcal{L}_{CAA}(\theta | \mathbf{Y}^{CAA}) = -\sum_{y} \sum_{s} \sum_{a} \hat{p}_{s,a,y} \ln\left(p_{s,a,y}\right)$$

2.5.5 EM total log-likelihood

The objective function of the EM is the joint negative log-likelihood of the HSP data, the CAA data and also a random effects term for estimation of recruitment deviations

$$\mathcal{L}_{joint}(\theta|\mathbf{Y}) = \mathcal{L}(\theta|\mathbf{Y}^{CAA}) + \mathcal{L}(\theta|\mathbf{Y}^{HSP}) + \mathcal{L}(\theta|\mathbf{Y}^{RE})$$

Here the last component is the contribution of the random effects on recruitment to the joint log likelihood. This is given by $\mathcal{L}(\theta|\mathbf{Y}^{RE}) = -\sum_y \log\left(\mathcal{N}\left(r_y, \sigma_R^2\right)\right)$ where $\mathcal{N}(.)$ denotes a Gaussian likelihood function.

2.6 Design structure

The study design specifies the intensity of sampling effort in terms of number of tissue samples to be taken each year and the number catch-at-age samples taken from the fishery.

In theory every CAA sample could be sampled for DNA, however each sample will take a cost to process. Therefore, the number of samples is a big driver of the cost of a project and so we want to set a target number of samples that is expected to provide useable results. In other words, we want to understand, given a plausible population of shortfin mako in the IO, what amount of sampling would likely provide a sufficiently accurate estimate of abundance or other metrics that would inform any future potential management decisions or monitor population status.

The design inputs for CKMR sampling specifies

- c_1, c_2 - these are the cohorts/ sampling years
- $N(S)_{c_1,c_2}^{CKMR}$ - the number of tissue samples taken from these years

It is important to note that age or sex specific sampling was not considered in this study. This is because SMA are a bycatch species and there is no reason to consider designs that target a particular range of sizes / ages. Instead, we assumed that the sample ages were set by the proportions of ages expected in the catch. In other CKMR design studies focusing on target species, there is scope to consider particular age ranges in sampling. In the case of bycatch species, there is limited ability to dictate the age range being encountered and the more likely situation is that a study would want to consider every sample it could obtain.

2.6.1 Design sample sizes

Design inputs for the CAA data were similar in this regard. We assume that both sexes are sampled equally and that sampling is dictated by an Effective Sample Size (ESS) number taken each year - labelled $N(S)_y^{CAA}$.

In all scenarios considered here, we applied the model over the same sequence of years:

- The model was initialized to start in 2020 and run forward with CAA data until 2026 when we assume CKMR tissue sampling starts. CAA sample sizes remained constant throughout the 20-year model period and a range of sample sizes were tested

- Tissue samples were modelled as being collected at a constant sample size for 5 years to 2031.

The sample sizes for CAA and HSP data are shown in Table 2.2.

Table 2.2: Configurations of base case design exploration. $N(CAA)$ *gives the number of CAA samples used in that run (these were simulated as being collected for 2020 to 2031).* $N(DNA)$ *denotes the number of tissue samples simulated as being collected over the years given in the sample years (middle) column*

N(CAA)	Sample years	N(DNA)
50	2026 → 2031	1000
75	2026 → 2031	1000
100	2026 → 2031	1000
150	2026 → 2031	1000
50	2026 → 2031	2000
75	2026 → 2031	2000
100	2026 → 2031	2000
150	2026 → 2031	2000
50	2026 → 2031	3000
75	2026 → 2031	3000
100	2026 → 2031	3000
150	2026 → 2031	3000

For each scenario in Table 2.2, n_{rep} = 1000 replicate OM / EM runs were carried out. The estimated values of parameters $\hat{\theta} = \left(N_0^f, M, \sigma_R\right)$ were stored. Average coefficient of variation values across the replicate runs were calculated as $\widehat{CV}(\theta_i) = 1/n_{rep} \sum \mathrm{SE}(\theta_i)/\bar{\theta_i}$ where $n_{rep} = 1000$ is the number of simulations. The average CV is intended as an approximate guide to the likely uncertainty on model parameters.

We examined relative errors on the following variables

- Exploitable biomass:

$$B_y^{exp} = \sum_s \sum_a N_{s,a,y}\, s_a W_{s,a}$$

- Number of mature animals

$$N_y^{mature} = \sum_s \sum_a N_{s,a,y}\, m_{s,a}$$

as well as $S_a = \sum_s S_{s,a}$. For each of the above model predicted quantity X^* we calculated a difference against the estimate $\hat{X}$ i.e. $X_i^* - \hat{X}_i$. The rationale for this was to examine the time trend in errors as data accrues over the course of sampling.

2.7 Uncertainty in population size

The uncertainty range in the latest stock assessment spans a large range. To demonstrate the potential for this to influence CKMR results, we ran two other scenarios on abundance: One where the $B_{2020}^{exp} \approx$ 20K tonnes to look at a lower population (relative to the assessment) than is expected, and another at $B_{2020}^{exp} \approx$ 150K tonnes to demonstrate the effect of a much larger population size. These values chosen were close to the upper and lower confidence bounds from the 2024 assessment. For these we conducted the same OM/EM approach as the base case above but only considered the case of $N(CAA) = 75$.

3 Results and Discussion

3.1 Existing length frequency data

The length frequency data from IOTC shows considerable variability in the number of length measurements collected between years (range: 83–1982). Converting these to ages using the growth model of Liu et al. (2018) gives the distributions shown in Figure 3.1. Aggregated together 50% of animals sampled were predicted to be less than 6.5 years and 80% were younger than 10 years old. While some parent offspring pairs might accrue from a 5-year sampling program (especially paternally, given the smaller size at maturity in males), these length/age distributions support the notion of models relying on HSPs.

To estimate the effective sample size of the distributions in Figure 3.1 would require dedicated modelling to and estimation of over-dispersion parameters (Candy 2008; Truesdell et al. 2017). However, the evident variability in sampling and at times very low sample size, does justify the use of a modest CAA ESS of 75 (Table 2.2) at least as a test of the robustness of the model. However, from 2012 to 2022 large sample sizes were collected which are likely to have a higher ESS.

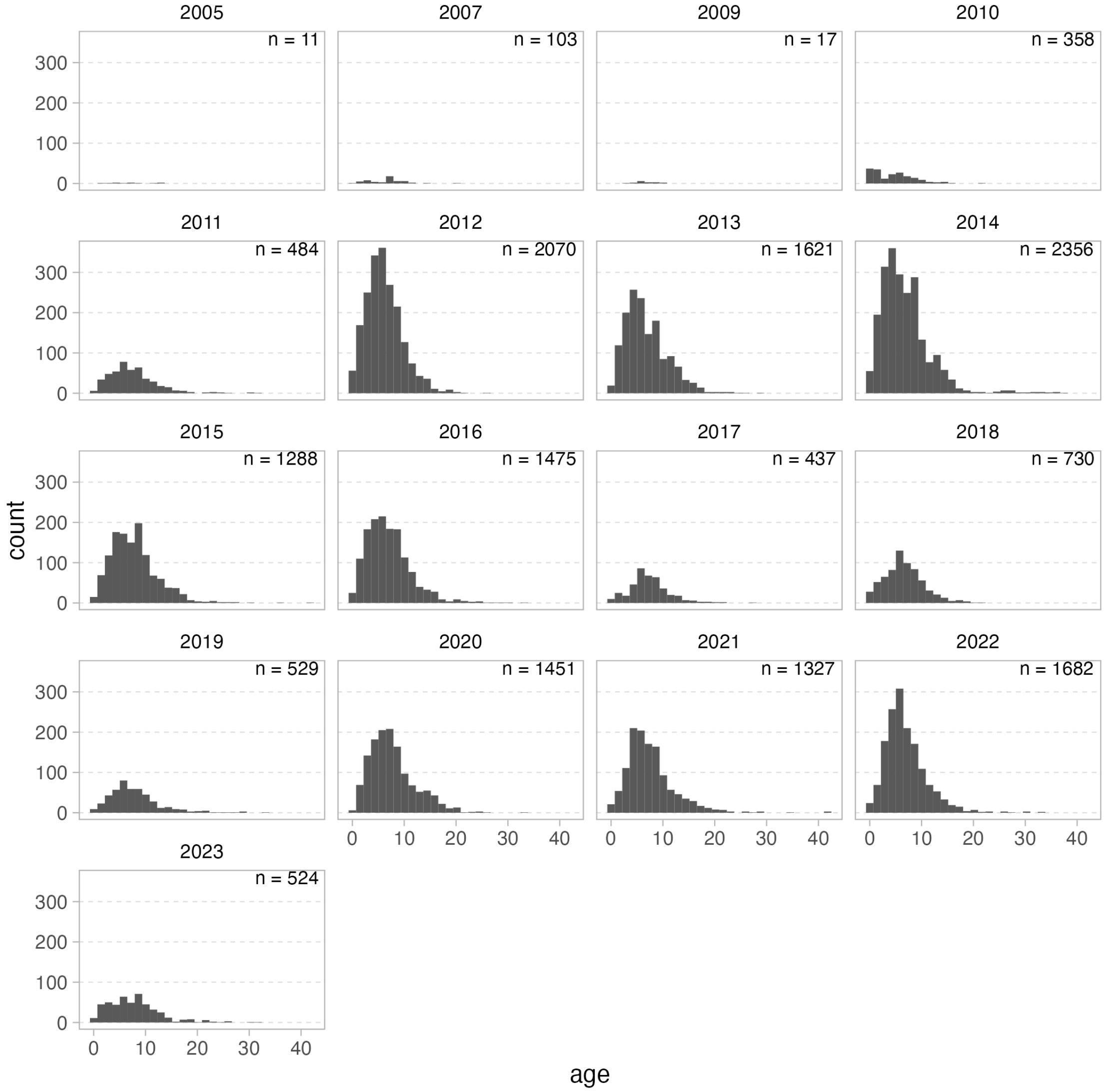

Figure 3.1: Existing length frequency data by year of collection (for IOTC species codes MAK, SMA and POR), with number of measurements included on the plot.

3.2 OM simulatioms

By selecting N_0^f and C_0 values that yielded approximate agreement with Coelho, Rosa, and Mourato (2024), a base case OM was configured to approximately reproduce the outputs of the 2024 stock assessment. Due to differences in structure and parameterisation between our age-structured model and the stock assessment surplus production model, the abundance and trends could not be precisely replicated. However, the approximate population size, throughout the OM model period was matched approximately to the assessment.

Initial simulations were investigated to determine the impact of different number of genetic samples on EM results. These simulations were conducted with an ESS of CAA data of N=75. Sensitivity to this value is explored in further analyses.

3.3 HSPs

Figure 3.2 shows how the number of HSPs observed in simulations increases with the number of genetic samples taken. Around 50 HSPs were detected when taking 1000 samples each year, ~150 for 2000 annual samples and ~350 for 3000 annual samples (Figure 3.2). These are lower than indicated in Table 1.1 but given the extremely unrealistic dynamics and assumptions in the simpler calculations, this is not unexpected. When more realism is added to the models, especially sexual dimorphism in maturity, the kinship probabilities change Given that the numbers are not massively different.

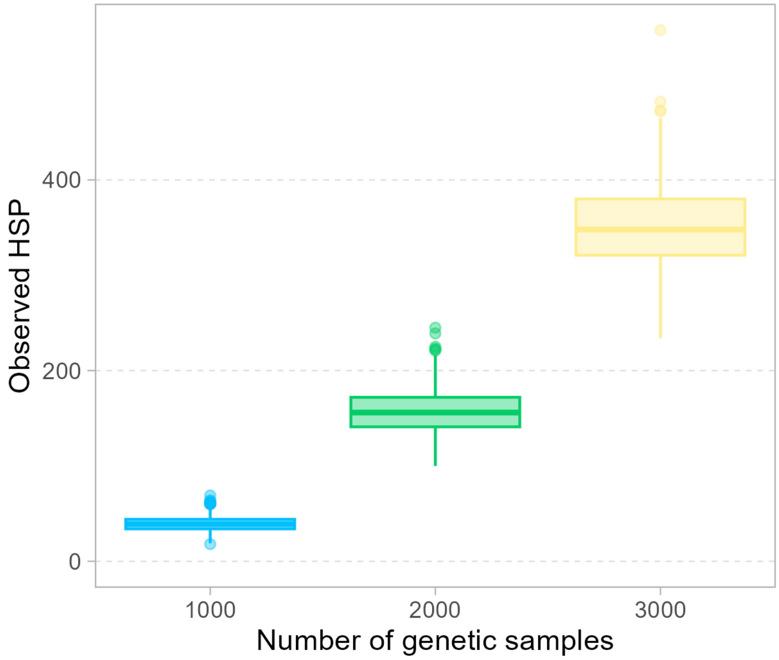

Figure 3.2: Boxplots of the number of observed HSPs from the simulations for each of the genetic sample sizes.

The EM was able to fit the provided data and estimate four parameters, the initial number of females N_0^f, the initial harvest rate h_{init}, natural mortality, M and recruitment variability standard deviation, σ_R.

Estimates from the EM were variable among simulations but always encompassed the OM (true simulated) value, with the peak of the distribution approximately matching the true value used in the OM for all parameters, except for σ_R (Figure 3.3). In this case, there was a large proportion of simulations where the estimate of σ_R approach 0. This is not a surprising result as the low level of variability in the OM does not provide a substantial increase in likelihood when fitting to data with low levels of variability. For this reason, σ_R is often a difficult parameter to estimate in stock assessments. Additionally, in any real assessment situation, there would be strategies for allowing for random recruitment variation through specification of a prior on σ_R.

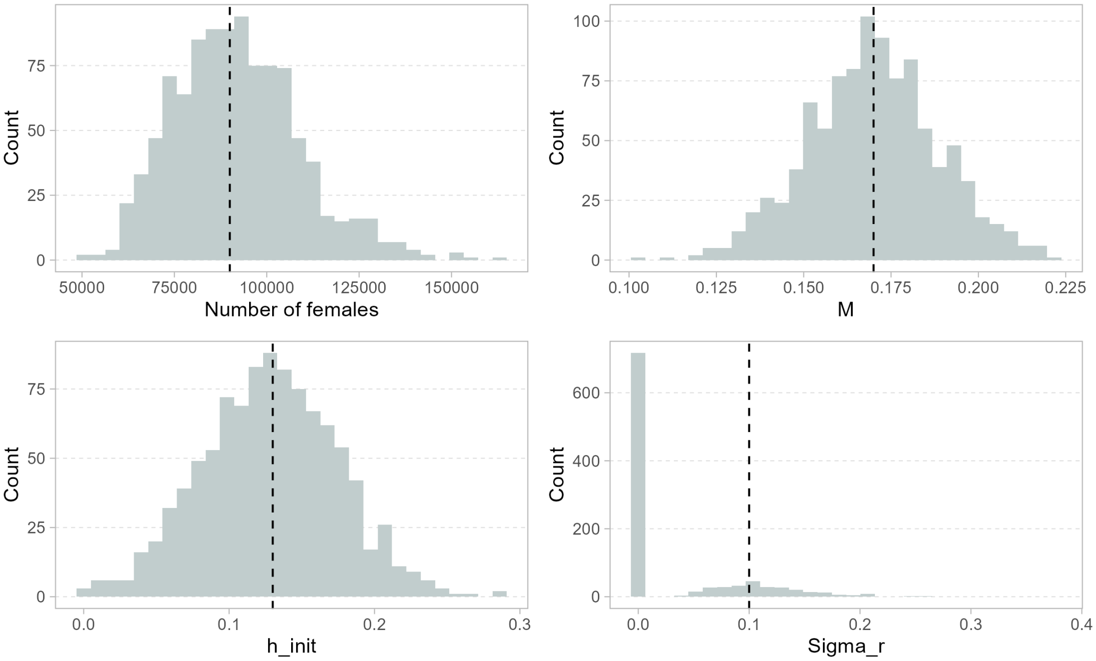

Figure 3.3: Histograms of the estimated parameters within the EM (bars) compared to the specified value in the OM (dashed line).

Trends in the total reproductive output S and exploitable biomass B_y^{exp} were relativity stable throughout the model period (2020 to 2036), with median estimates from the OM and EM almost identical, over the range of genetic sample numbers considered (Figure 3.4).

However, larger number of genetic samples reduced estimate uncertainty with a particularly large drop in uncertainty between 1000 and 2000 samples (Figure 3.4). There was less of a gain in information when comparing 2000 to 3000 levels. This is consistent with the notion that the addition of new kin pairs via more intensive sampling does not continue to add the same amount of information.

Based on the results in Figure 3.4 and noting the dependence on the assumptions driving the OM configuration, we would recommend collection of at least 2000 samples per year over the course of a 5-year sampling program. The corrollary of this, is that collection of significantly less than 2000 samples is likely to be riskier - i.e. is more likely to result in an uncertain estimate of population status.

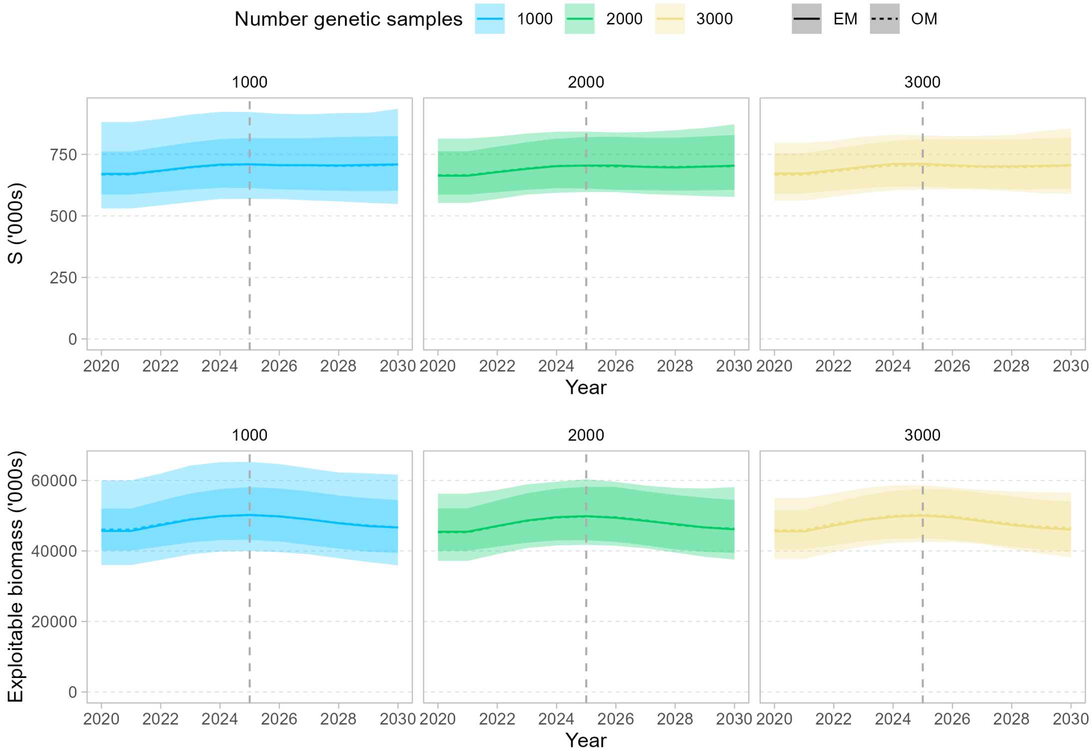

Figure 3.4: Estimates of S and exploitable biomass from the OM and EM. Lines are median values among simulations and shaded areas are 90% simulation intervals. The larger confidence intervals are for the EM.

Relative error, or difference between the OM and EM results showed no systematic trends throughout the model period for all variables investigated (Figure 3.5). The results do demonstrate that on average, simulations have a larger relative error when there are only 1000 genetic samples, compared to when there is 2000 or 3000 (Figure 3.5). This suggest that larger genetic sample sizes reduce the likelihood of model that are biased.

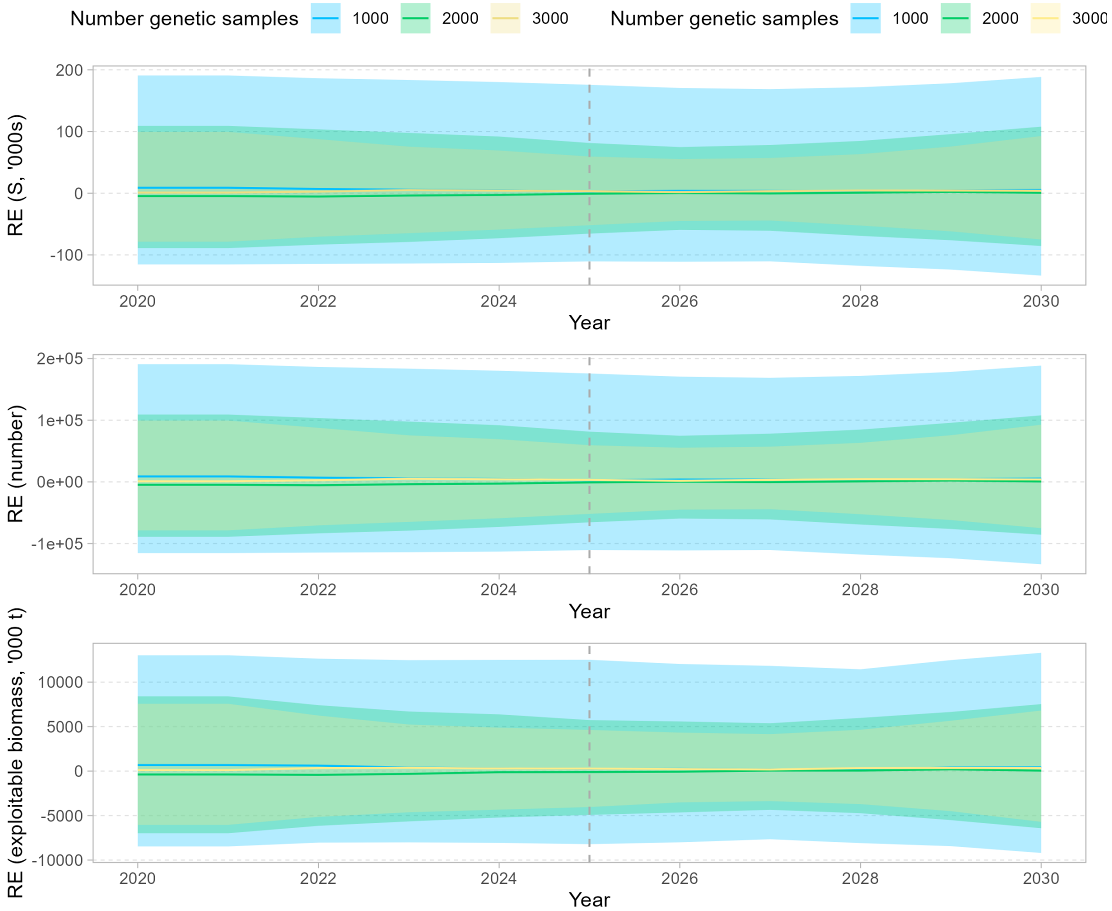

Figure 3.5: Estimates of S and exploitable biomass from the OM and EM. Lines are median values among simulations and shaded areas are 90% simulation intervals.

The CVs from the EM are often used to determine the appropriate number of genetic samples for CKMR design studies. The estimated CVs for all parameters decreased as the number of genetic samples increased, although this was particularly evident when moving between 1000 and 2000 samples annually, with a smaller difference between 2000 and 3000 annual samples (Figure 3.6). On average across the various model outputs investigated CVs were generally at or below 0.1 when at least 2000 annual samples were collected (Figure 3.6). When considering this is combination with the time series and relative error plots presented above, that showed reduced variability in OM/EM differences with 2000 or more samples, it suggests that a minimum of 2000 annual samples over 5 years would be required to obtain a robust estimate of absolute population size. Note in Figure 3.6 that the recruitment estimates are less influenced by increased genetic sample size. This reflects the fact that CKMR data informs mostly on the adults, whereas the fixed CAA sample size which informs on the rest of the population.

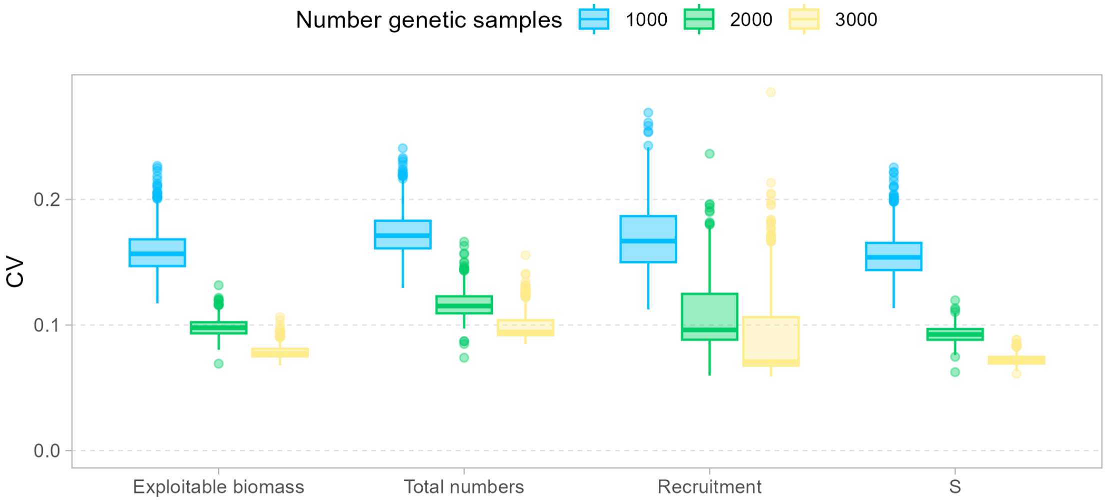

Figure 3.6: Boxplots of estimated CVs from the EM for key outputs of the population dynamics model for each of the genetic sample sizes tested.

3.3.1 Sensitivity to CAA sample sizes

Additional simulations were conducted to test the impact of varying the number of CAA samples obtained throughout the model period. CAA effective sample sizes of 50, 75, 100 and 150 were conducted. Estimates of *S* throughout the model period were relatively stable with almost no difference between OM and EM median values by the number of annual genetic samples, or by CAA ESS (Figure 3.7). There was reduced 90% simulation intervals to those similar to the EM when collecting at least 2000 annual genetic samples, however, none of the CAA ESS values investigated impacted these results (Figure 3.7). Therefore, we observed incremental reduction in CVs of all model outputs as the CAA ESS increased, although the difference is relatively minor when compared with the decrease from increasing the number of annual genetic samples (Figure 3.7). This suggests that the results of a CKMR assessment model would be relatively robust to lower number of length samples, however, there is benefit from sampling as many individuals as practicable.

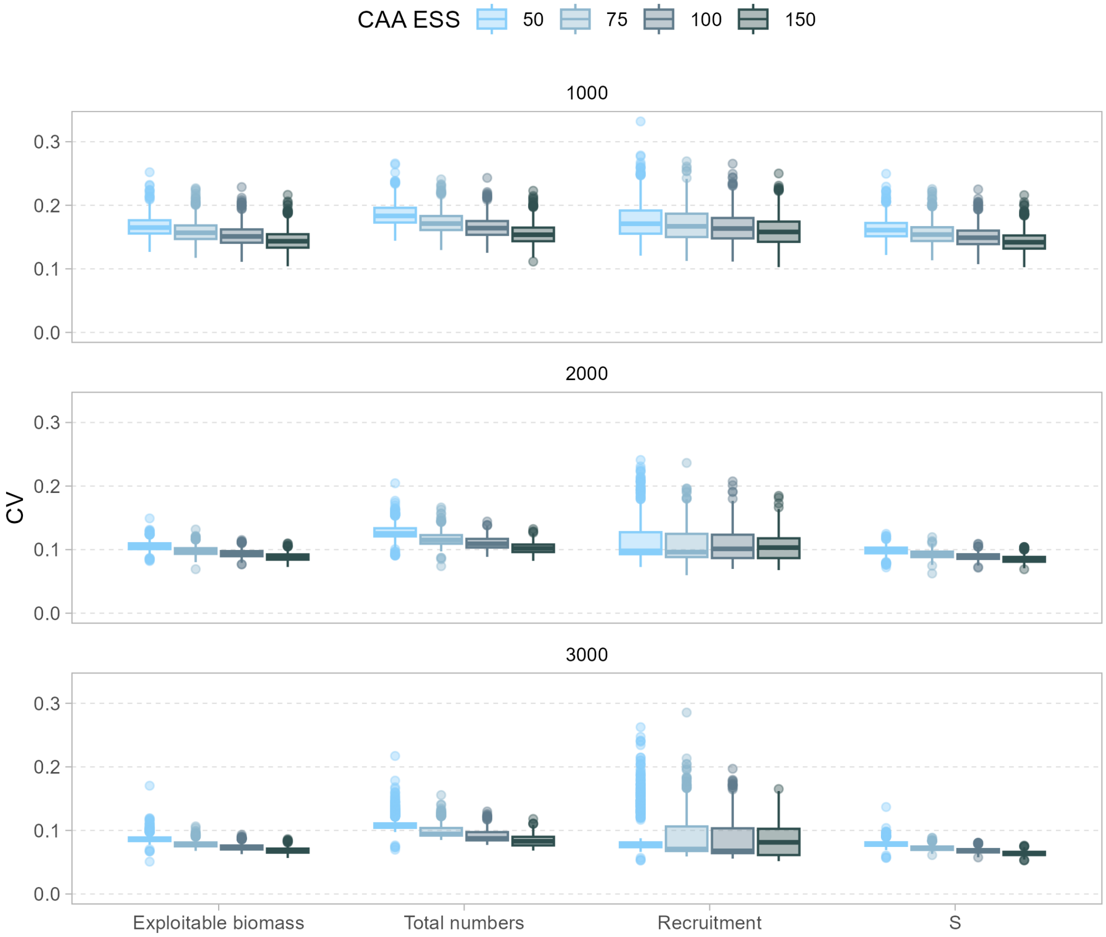

Figure 3.7: Boxplots of estimated CVs from the EM for key outputs of the population dynamics model with panels for each of the annual genetic sample sizes tested, while different CAA effective sample sizes (CAA ESS) are demonstrated by colour.

This picture was also reflected in the estimated trajectories of TRO (S), which were reasonably well estimated on average for all combinations of genetic sampling and CAA sampling considered. However, it was again clear that the uncertainty on the EM estimates is most influenced by the amount of genetic tissue samples. Given that in practice, each tissue sample should have an accompanying length measurement, then 2000 tissue samples, for example, should imply 2000 length measurements which can be converted to ages. We emphasize again, that uncertainty in ageing would most likely need to be accounted for in a real model.

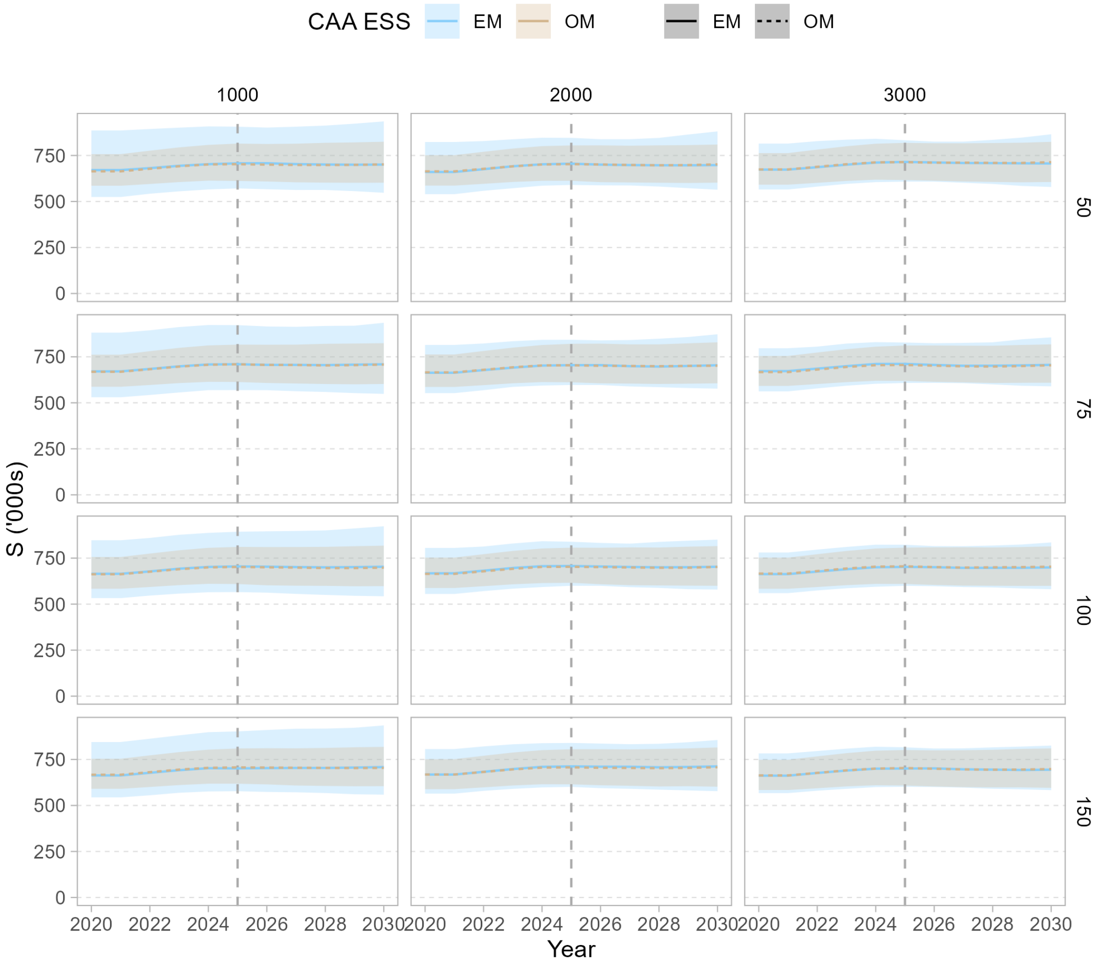

Figure 3.8: Simulated and estimated annual averages of population trajectory over all simulations at three levels of genetic sampling and four levels of CAA sampling. .

3.3.2 Alternative population sizes

The effect of lower and higher than expected population sizes on the parameter CVs is show in Figure 3.9. As per the general principles of CKMR, the lower population size generates more HSPs and gives a higher precision estimates (median CV on all quantities < 0.1 - figure 3.9). This rises in the upper case to median CVs between 0.1 and 0.2 on all model quantities.

This is a general result with CKMR, for a fixed sample size, precision increases at smaller adult population sizes. Therefore, in the case considered here, where the concern is that the population is declining, then the results suggest a CKMR assessments would provide solid evidence of low population sizes. In the converse situation, the uncertainty would rise, but there would still be a signal suggesting a large population size.

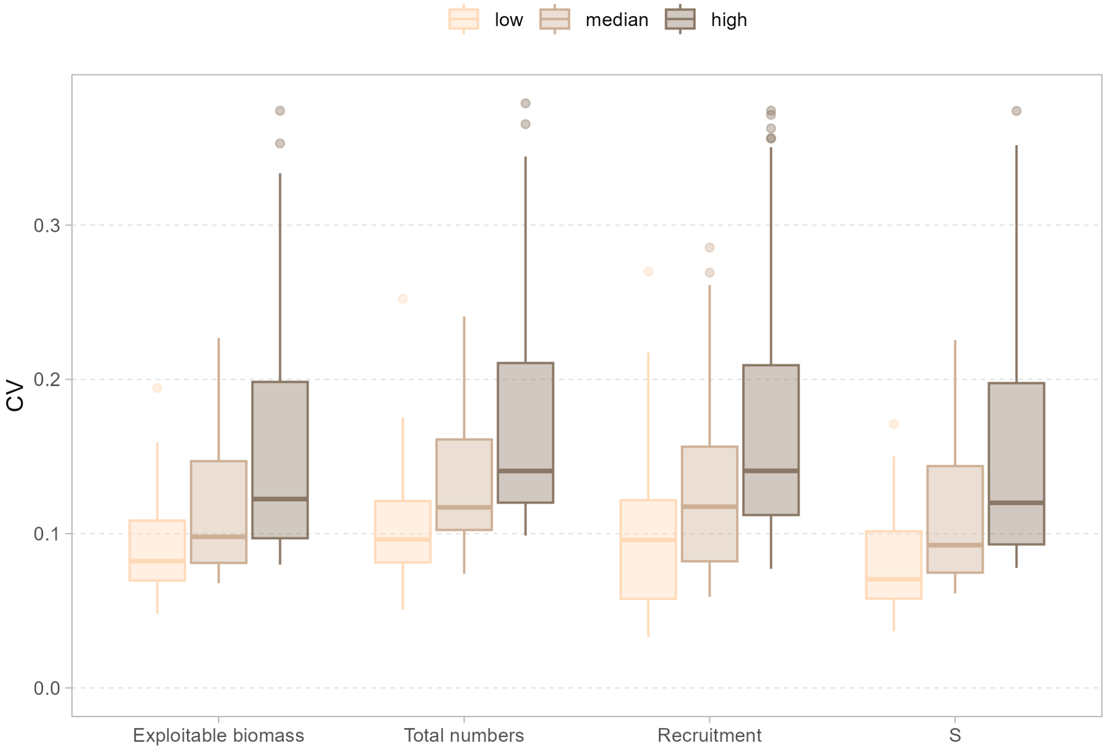

Figure 3.9: Boxplots of estimated CVs at three levels of population size (OM tuned so that B_{2020}^{exp}*; low ≈ 20 k tonnes, median ≈ 50 k tonnes and high ≈ 150 k tonnes)*

Plots of simulated/estimated population Figure 3.10 trajectories through time, indicate that more certain results are obtained at lower population sizes, and that there is much higher band of uncertainty for the high population size at low sample size. Nevertheless, and again noting all the aforementiond assumptions surrounding the OM model tuning, the CKMR/CAA data combination is able to estimate the population dynamics reasonably well at 2000 and 3000 annual tissue samples, even at the larger population levels.

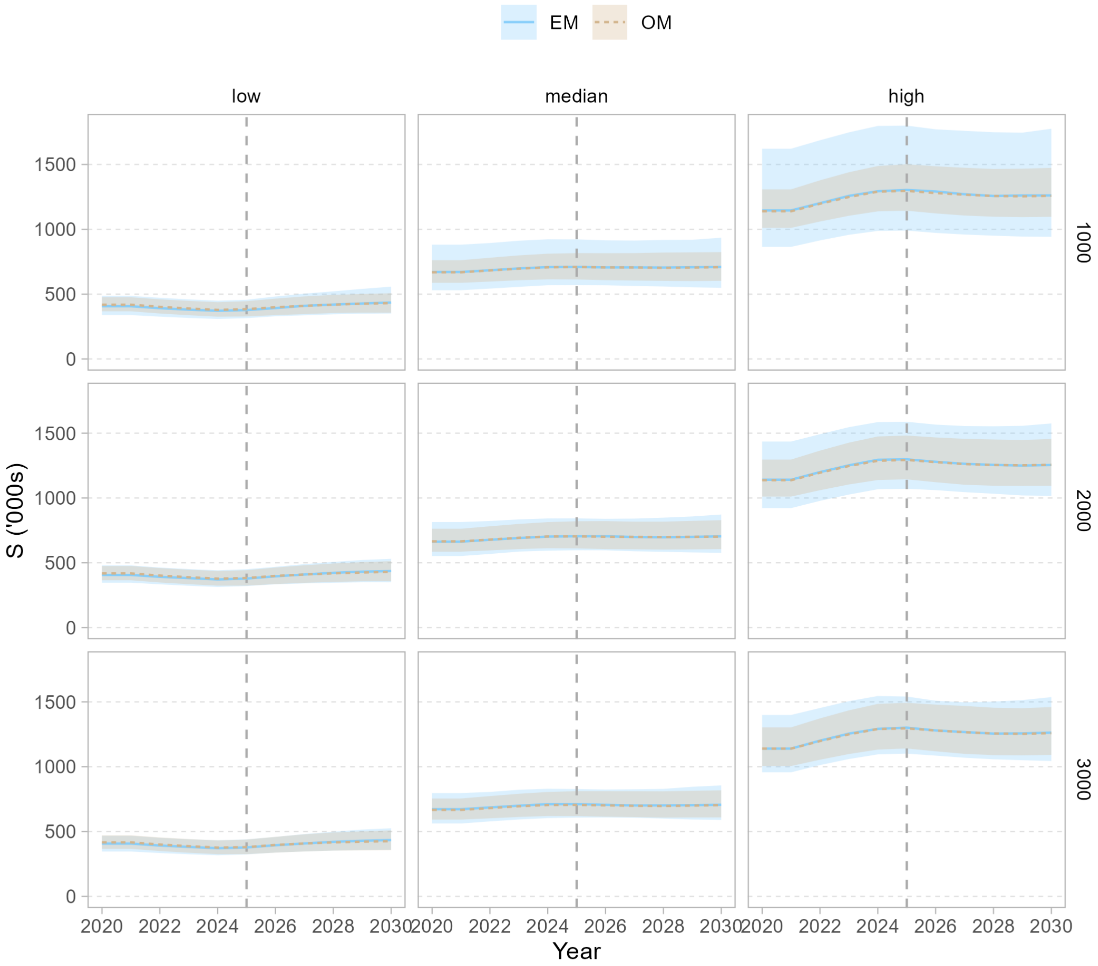

Figure 3.10: Summaries of fits through time at three levels of population size (OM tuned so that B_{2020}^{exp}*; low* $\approx 20kt, median \approx$ *50 kt, and high ≈ 150 kt)*

4 Conclusions

To the extent possible given the paucity of informative data on SMA population status, the modelling in this paper was conducted to approximate the most recent IOTC assessment (Coelho, Rosa, and Mourato 2024) of SMA. If this assessment is roughly representative of the true abundance of SMA in the IO, then our results indicate that a sample size of around 2000 tissue samples per year would provide informative sibling pair data. Moreover, the length sampling would need to occur with the tissue collection, which means that the CKMR sampling should also produce sufficient CAA data to produce an informative assessment of SMA populations in the Indian Ocean.

The time frame considered here was 5 years of tissue sample collection. In reality, a CKMR project would examine the hit-rate of HSPs through the period of sampling and the early results would inform on whether the sampling size and timelines were likely to be sufficient. CKMR can therefore be adaptive as information is collected, with potential to increase or even reducing, sample rate collection. In addition, if long term sampling was adopted to inform estimates of stock size in an ongoing manner, the number of annual samples required would decrease through time.

Catch-at-age data is important for providing information on recruitment and harvest rates – which CKMR cannot do. It is important to note that understanding recruitment dynamics are particularly important for SMA given its life-history. Recent ICCAT assessments indicated that as the cryptic spawning biomass dies off naturally the recruitment would be severely impaired because high fishing pressure on the juveniles meant that there were few individuals replenishing the spawning biomass stock. Our analysis indicated that the results are relatively robust to CAA ESS, although better sampling is always going to improve model estimates - particularly those related to recruitment. Although we cannot say definitively, the modelling indicated that sampling intensity of length frequency data over recent years is likely to be sufficient inasmuch as it demonstrates that small ESS are sufficient to inform a model like that implemented here.

We do note that the modelling presented here is somewhat artificial in that we have not estimated selectivity, ESS dispersion parameters, accounted for ageing errors and other complications that would arise in a real integrated assessments utilising CKMR and age distribution data (e.g. Thomson et al. 2020; RM Hillary et al. 2023). In our study we aimed to consider a model that captures key aspects of real CKMR assessments, while minimising speculation on how these issues may manifest in a real study.

It is also worth noting that a simpler modelling approach could be investigated. For example, simpler population models, which only model number of adults and without including age structure has been applied to various shark species of conservation concern (Bruce et al. 2018; Hillary et al. 2018; Patterson, Hillary, Kyne, et al. 2022). Assuming that the structure of these models does not egregiously contradict assumptions, such models estimate the size of the breeding population - which at the moment would be a major step forward in understanding SMA populations. But given that to get useable CKMR data requires an age estimate (typically inferred based on length), then at the sample sizes envisioned for SMA (N >2000), then CAA data would already be generated. Given this data would be useful for understanding juveniles and recruitment, we did not investigate simpler model structures in this study.

Similarly, given that there is no clear picture of spatial structure apparent in IO SMA (see Patterson et al, IOTC-2025-WPEB21(AS)-41). we did not consider spatial models of the sort used in Hillary et al. (2022). The main point of this study was to advise on sample size required to obtain population size estimates.

From a purely operational perspective, obtaining 2000 samples per year would be a large, but not insurmountable task, and there are likely to be sufficient interactions with SMA. The length frequency data in IOTC data repositories shows that in some years, roughly this number of measurements of SMA were taken.

However, this statement does not account for how management provisions such the measures outlined in IOTC Resolution 25/09 (https://iotc.org/sites/default/files/documents/compliance/cmm/iotc_cmm_2509_0.pdf) may add challenges to obtaining samples. Further complications for sampling and logistics arise from SMA being listed under CITES Appendix II. While these measures are a in straightforward response to concerns regarding SMA declines, they are a challenge for implementation of effective CKMR sampling programs, which is the only current method which could significantly improve scientific monitoring of their population size.

While the situation is complex, it is worth noting that retention bans will also make CPUE series even more problematic for inclusion in future stock assessments as they will represent a fundamental shift in the data series and mean that post-ban catch and effort data is not comparable to pre-ban data, and likely to be even less informative for assessment purposes. Nevertheless, it is inevitable that while high-seas tuna fleets operate, interactions with SMA and other pelagic sharks will continue. This combination of contining bycatch and simultaneous ongoing degradation in already uninformative data sources creates a clear barrier to effective monitoring to inform science-based management of SMA and other pelagic shark bycatch issues.

5 Acknowledgements

This project was supported by funding from the European Union. This document has been produced with the financial assistance of the European Union. The views expressed herein can in no way be taken to reflect the official opinion of the European Union. We gratefully acknowledge input and assistance from Richard Hillary, Denham Parker and Ash Williams from CSIRO. Laura Tremblay-Boyer and Campbell Davies from CSIRO were instrumental in developing this project. We also thank Lauren Nelson, Paul de Bruyn and Dan Fu of the IOTC for their assistance.

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For further information

CSIRO Environment
Toby Patterson
+61 03 62 325408
Toby.Patterson@csiro.au

Pia Bessell-Browne
+61 03 6232 5100
Pia.Bessell-Browne@csiro.au